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Re-Engineering the Stomatopod Eye

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Final Report

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14. ABSTRACT <p>This final report (2013-2016) is a comprehensive summary of our efforts over the course of this grant. It focuses on the Cronin laboratory but includes work for the comprehensive four-team effort (also including Marshall's team in Australia, Roberts's team in England, and Gruev's team - subcontracted to Cronin - in St Louis, Missouri). Altogether the Cronin laboratory published some 36 papers, book chapters, or books from the middle of 2013 to the end of 2016 (the team as a whole has a total of some ~80-90 unique publications in this time). We have been completing our work on the opsin diversity in mantis shrimp eyes, with a strong focus on the opsins devoted to polarized-light vision, including our finding that polarized-light receptors contain an unusually large number of co-expressed opsin genes (this work has been ongoing since ~2007 or so). We have also greatly expanded our understanding of ultraviolet vision in stomatopods, including UV vision devoted to polarized-light analysis. The work has led to the discovery of a new class of filters used in animal eyes to control the detection of multiple bands of ultraviolet light, including polarized ultraviolet, published in 2014 and 2015. We have continued to develop field-capable, user-friendly, real-time polarization cameras in collaboration with our subcontractor Viktor Gruev and his students, used for visualizing environments, terrain, and animals in natural settings, and also extending this work to preliminary studies of polarization patterns in stomatopods and cephalopods.</p>			
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FINAL REPORT
AFOSR Award Number FA9550-12-1-0321

"Re-engineering the Stomatopod Eye"

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Objectives (*as stated in the original proposal*)

(1) To learn the design foundations stomatopods use for optimized, rapid processing of multi-channel information. We will examine the limits of resolution polarization vision in stomatopods, using new methods of presenting stimuli that provide precise tuning of stimulus polarization angle, degree and ellipticity. Similar approaches permit us to explore spectral resolution and see further through scattering media. Central to this objective is discovering how stomatopods scanning eye behaviour organizes and inputs multi-channel spatiotemporal information.

(2) To discover how information is processed in stomatopod visual systems. At the most fundamental level we will undertake studies of the molecular and cellular basis of rapid photoreception and phototransduction (by examining the genes and cytoskeletal elements of mantis shrimp receptors). At higher levels, we will examine neural interconnectivity and processing principles at various stages of analysis in the visual system both anatomically and with electrophysiological approaches.

(3) To discover the natural complexity of visual scenes the stomatopod imaging system has evolved to see. It is fundamental that we understand the visual information stomatopods see. This crucial component of the project takes findings generated by the above-stated objectives, with inspiration from our earlier work as well, to inform the design of artificial stomatopod inspired imaging devices. Our findings related to camouflage patterns or biological communication systems will inspire future image analysis of natural and machine vision environments.

(4) To investigate the co-evolution of visual systems, visual signals and camouflage in the natural environment. We will proceed from the above discoveries to relate how stomatopods see and what they see to our observations that species vary in the types of signals they produce (including spectral, polarization, circular polarization, and temporal motion features). We will examine whether polarization signals are matched to properties of the polarization receptors among species, and detail the evolutionary paths of the optical devices in stomatopod eyes, polarization sensitivity and polarization signals.

Status of Effort (Abstract)

This final report (2013-2016) is a comprehensive summary of our efforts over the course of this grant. It focuses on the Cronin laboratory but includes work for the comprehensive four-team effort (also including Marshall's team in Australia, Roberts's team in England, and Gruev's team - subcontracted to Cronin - in St Louis, Missouri). Altogether the Cronin laboratory published some 36 papers, book chapters, or books from the middle of 2013 to the end of 2016 (the team as a whole has a total of some ~80-90 unique publications in this time). We have been completing our work on the opsin diversity in mantis shrimp eyes, with a strong focus on the opsins devoted to polarized-light vision, including our finding that polarized-light receptors contain an unusually large number of co-expressed opsin genes (this work has been ongoing since ~2007 or so). We have also greatly expanded our understanding of ultraviolet vision in stomatopods, including UV vision devoted to polarized-light analysis. The work has led to the discovery of a new class of filters used in animal eyes to control the detection of multiple bands of ultraviolet light, including polarized ultraviolet, published in 2014 and 2015. We have continued to develop field-capable, user-friendly, real-time polarization cameras in collaboration with our subcontractor Viktor Gruev and his students, used for visualizing environments, terrain, and animals in natural settings, and also extending this work to preliminary studies of polarization patterns in stomatopods and cephalopods. We collected hours of polarization video in marine and terrestrial environments and have just published a paper on the polarization properties of fishes in clear marine waters in the prestigious journal *Current Biology*. From this work, we have finally begun to work out the utility and the limits of polarization imaging and polarization camouflage in marine animals, which led to a major critique published this year in *Science* (and to a future review in the *Journal of Experimental Biology*). The imaging work was awarded IEEE's 2016 IEEE Donald G. Fink Award. The Gruev team is also exploring the possibility of using polarization imaging as a tool for underwater navigation. The team as a whole has met repeatedly to conduct research every year and to plan ahead, including a meeting with the AFOSR program fundees at Eglin AFB in October 2013 and 2014 and in Arlington in 2015. We conducted joint field trips to the Great Barrier Reef in 2013, 2014, and 2015. In addition to this, Cronin and his students and postdoc attended numerous meetings nationally and internationally in 2013-2016.

A summary of our results will be described in detail in the next section.

Accomplishments/New Findings

1. Hiroko Awata, the postdoctoral fellow who was previously funded by this award, completed her research into the molecular genetics of opsins of stomatopod crustaceans. She (together with Megan Porter and Michael Bok, previous members of the lab) is preparing a manuscript on the expression patterns of mantis shrimp opsins, completing an eight-year project to discover where each opsin is expressed. Her results are particularly interesting in that they show that multiple opsins are expressed in polarization receptors in stomatopods. She also found evidence for the presence of a "dorsal rim" – a specialized region of the retina that in insects is devoted to polarization vision.

2. Nicholas Roberts, at the University of Bristol in the UK, continues our long-term collaboration on the biology and physics of polarized-light reception with joint funding for EOARD. Regarding our particular part of the grant, Nick's group continues to be involved in studies of the photonic nature of polarization reflectors and interference filters in stomatopod adult and larval eyes. He has also been involved in our work on the evolution of polarization signals in animals and in the unique eye movements, work that is now published. Nick's group continues to join with Justin and me in the US, England, and Australia. Mary Durham, a former member of my lab group, is preparing a manuscript on scanning movements of stomatopod eyes related to the Roberts research (Fig. 1).

3. Michael Bok, a 2013 PhD graduate of the laboratory, completed his thesis work on the properties of ultraviolet (UV) polarization receptors in mantis shrimps, and is now a postdoc with Dan-Eric Nilsson in Lund, Sweden. As a postdoc, he continues his work on the properties of UV opsins and UV receptors (including polarization receptors) in mantis shrimps. Mike and I completed a review of ultraviolet photoreception and vision throughout animals this year, now in press.

4. Our work with Viktor Gruev (now at the University of Illinois Urbana Champaign) on polarization imaging and display systems has been extremely successful. Viktor and two of his students have spent several weeks with Justin, Nick, and me in the field in recent years working on projects and questions of mutual interest. This has led to superb new field polarization imaging systems, resulting in a prize-winning paper in IEEE. Gruev has extended his use of polarization imaging to underwater navigation (Fig. 2), and his team continues to improve the utility of polarization imaging underwater for imaging, viewing, reconstructing scenes, and facilitating navigation.

5. Our work with the Justin Marshall laboratory at the University of Queensland continues to be unusually successful and satisfying, as it has been for a very long time already. Justin and I finally completed our work on the jointly authored book *Visual Ecology* during the term of this funding. (published by Princeton University Press, this book was awarded the 2015 PROSE award for Best Textbook in Biological and Life Sciences). Justin and I continue to exchange students and have jointly written numerous book chapters and papers resulting from AFOSR funding in this cycle.

6. Another author of the *Visual Ecology* book, Sönke Johnsen (who is also an AFOSR awardee for work on magnetic-based navigation), has become a valuable collaborator in our work, particularly with Justin Marshall and me. We published an article in *Current Biology* in 2016 that overturns the long-held idea that animals using polarization vision in water can see fish further than those using brightness vision alone (Fig. 3A). We also published a technical comment in *Science* showing that an earlier paper published in that journal reached highly erroneous conclusions regarding a concept those authors wrongly called "polarocrypsis" (Fig. 3B).

6. We continued our work with Roger Hanlon's laboratory at MBL Woods Hole, on non-visual opsins of cephalopods and fishes. My recently graduated PhD student, Alexandra Nahm worked on this project, mostly with separate funding. However, as it appears that the cephalopods use identical opsins in their retinas and in their skin tissues, and we know the retinal opsins are designed to form multimeric polarization-oriented complexes, we are very interested to learn how these opsins are deployed in the distributed skin sensors in these animals. Alex helped to supervise a new PhD

student in the lab, Mary Donohue, who is studying the extraocular opsins of mantis shrimps as expressed in their central nervous systems.

7. Kate Feller, a former doctoral student in my laboratory (some of her research was supported by AFOSR), completed her thesis research on eye development in mantis shrimps and other crustaceans and joined Nick Roberts's laboratory in Bristol to continue to study photonic properties of reflectors in crustacean eyes. She now works with Paloma Bellido Gonzalez at the University of Cambridge. Her work has elucidated the molecular diversity in the retinas of these animals and will produce a much better understanding of the development of polarization vision and of the roles of polarization opsins in larval and adult eyes, as well as of several very exotic photonic devices found in larval eyes.

8. A new postdoctoral fellow, Chan Lin, joined the lab with AFOSR support in October, 2014. Chan completed his PhD in Nick Strausfeld's laboratory, University of Arizona, and his specialty is neuroanatomy of arthropod central nervous systems and visual neuropils. He is working on the neuroanatomy of stomatopod visual centers and on the development of stomatopod vision. His work on the neuroanatomy of developing visual analysis networks in stomatopod larvae and young adults is described in an appendix to this report (see Appendix I).

Personnel Supported

Principal Investigator:

Thomas W. Cronin, Department of Biological Sciences, UMBC (summer salary)

Postdoctoral Fellows:

Hiroko Awata (From onset until March 2014; full salary support)

Chan Lin (Joined the lab in October 2014; full salary support)

Graduate Students:

Michael Bok (UMBC PhD student to 2013, research support)

Kate Feller (UMBC PhD student to 2014, research support)

Alexandra Nahm (UMBC PhD student to 2015, research support)

Mary Willard (current UMBC PhD student, research support)

Alice Chou (current UMBC PhD student, research support)

Ricky Patel (current UMBC PhD student, research support)

Undergraduate Students (Research projects related to the AFOSR grant):

Taylor Radden (former UMBC junior, MARC minority student)

Zoe Garcia (former UMBC freshman, Meyerhoff scholar)

Anyia Byrd (current UMBC sophomore, Meyerhoff scholar)

Publications (* indicates AFOSR support; ** indicates fully funded by AFOSR. Reprints available on request)

1. *T.W. Cronin, J.I. Fasick, L.E. Schweikert, S. Johnsen, L.J. Kezmoh and M.F. Baumgartner. 2016. Coping with copepods: do right whales (*Eubalaena glacialis*) forage visually in dark waters? Philosophical Transactions of the Royal Society (in press).
2. T.W. Cronin and M.J. Bok. 2016. Photoreception and vision in the ultraviolet. Journal of Experimental Biology (in press).
3. **S. Johnsen, Y. Gagnon, N.J. Marshall, T.W. Cronin, V. Gruev, S. Powell. 2016. Polarization vision seldom increases the sighting range of silvery fish. Current Biology 26, R752-R754.
4. **T.W. Cronin, Y. Gagnon, S. Johnsen, N.J. Marshall, and N.W. Roberts. 2016. Comment on “Open-ocean fish reveal an omnidirectional solution to camouflage in polarized environments”. Science 353, 552a. <http://dx.doi.org/10.1126/science.aaf4481>
5. **I.M. Daly, M.J. How, J.C. Partridge, N.J. Marshall, T.W. Cronin, and N.W. Roberts. 2016. Rolling their eyes: dynamic polarization vision in mantis shrimps. Nature Communications 7, 12140. doi:10.1038/ncomms12140
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7. *A.C.N Kingston and T.W. Cronin. 2016. Diverse distributions of extraocular opsins in crustaceans, cephalopods, and fish. Integrative and Comparative Biology (in press). doi:10.1093/icb/icw022
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13. B.E. Dalton, J. Lu, J. Leips, T.W. Cronin, and K.L. Carleton. 2015. Variable light environments induce plastic spectral tuning by regional opsin coexpression in the African cichlid fish, *Metriacroma zebra*. Molecular Ecology 24, 4193-4204. Doi: 10.1111/mec.13312
14. *A.C.N. Kingston, A.M. Kuzirian, R.T. Hanlon, and T.W. Cronin. 2015. Visual phototransduction components in cephalopod chromatophores suggest dermal photoreception. Journal of Experimental Biology 218, 1596-1602. doi:10.1242/jeb.117945
15. **M.J. Bok, M.L. Porter, and T.W. Cronin. 2015. Diversity, ecology, and evolution of ultraviolet filters in stomatopod crustaceans. Journal of Experimental Biology 218:2055-2066. doi:10.1242/jeb.122036
16. *D.B. Zurek, T.W. Cronin, L.A. Taylor, K. Byrne, M.L.G. Sullivan, and N.I. Morehouse. 2015. Spectral filtering enables trichromatic vision in colorful jumping spiders. Current Biology 25: R1-R3.
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18. **K. Feller, J. Cohen, and T.W. Cronin. 2015. Seeing double: visual physiology of double-retina eye ontogeny in stomatopod crustaceans. Journal of Comparative Physiology A 201:331-339.
19. B. Dalton, E.R. Lowe, T.W. Cronin, and K.L. Carleton. 2014. Spectral tuning by opsin coexpression in retinal regions that view different parts of the visual field. Proceedings of the Royal Society B 281: 20141980.
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28. **K.D. Feller and T. W Cronin. 2014. Hiding opaque eyes in transparent organisms. *In situ* spectral and image contrast analysis of eyeshine in stomatopod larvae. *Journal of Experimental Biology* 217, 3263-3273.
29. **M.J. How, M.L. Porter, A. Radford, Kathryn Feller, S. Temple, R.L. Caldwell, J. Marshall, T.W. Cronin, and N.W. Roberts. 2014. Out of the blue: The evolution of horizontally polarized signals in *Haptosquilla* (Crustacea, Stomatopoda, Protosquillidae). *Journal of Experimental Biology* 217, 3425-3431. doi:10.1242/jeb.107581
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31. T.W. Cronin, S. Johnsen, J. Marshall, and E.J. Warrant. 2014. *Visual Ecology*. Princeton University Press. 405 pp. Winner of the 2015 PROSE Award for best Textbook: Biological and Life Sciences
32. T.W. Cronin and R.H. Douglas. 2014. Seeing and doing: how vision shapes animal behavior. *Philosophical Transactions of the Royal Society B* 369: 20130030. <http://dx.doi.org/10.1098/rstb.2013.0030>
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Philosophical Transactions of the Royal Society B 369: 20130032.
<http://dx.doi.org/10.1098/rstb.2013.0032>

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36. *F.R. Schram, S.T. Ah Yong, S.N. Patek, P. A. Green, M.V. Rosario, M.J. Bok, T.W. Cronin, K.S. Mead-Vetter, R.L. Caldwell, G. Scholtz, K.D. Feller, and P. Abelló. 2013. Subclass Hoplocarida Calman, 1904: Order Stomatopoda Latreille, 1817. In: Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea. Vol. 4, Part A. (J. C. von Vaupel Klein, M. Charmantier-Daures, and F. R. Schram. Eds.). Brill, Leiden, pp. 179-355.

Interactions/Transitions (2016 only, see earlier reports for other years)

a. Participation/presentations at meetings, conferences, seminars, etc.

My postdoc Chan Lin prepared a poster for the SICB meeting, Portland OR, January 2016.
(presented by Cronin).

My PhD student Mary Donohue presented a poster on AFOSR-supported research at the SICB meeting, Portland OR, January 2016.

I presented a contributed talk in a symposium I co-organized on “Extraocular, Nonvisual, and Simple Photoreceptors” at the annual SICB meeting, January 2016.

My postdoc Chan Lin presented a poster at the meeting on Central Complex at Janelia Farm, Leesburg VA in March 2016.

My PhD student Alice Chou presented a poster at the meeting on Central Complex at Janelia Farm, Leesburg VA in March 2016.

My postdoc Chan Lin prepared a poster for the ICN meeting, Montevideo, Uruguay, March 2016.
(presented by Cronin).

I presented an invited talk at the University of California Irvine in May 2016.

I presented a talk at the workshop on Animal Camouflage and Signals held by the University of Exeter in Penryn, Cornwall, August 2016.

My former PhD student Alexandra Nahm presented a talk on AFOSR-supported research at the SICB meeting, Portland OR, January 2016.

My former student Mike Bok, M.J. gave an invited talk on AFOSR-related research at the Workshops in Ecology and Behaviour (WEB) Seminar, University of Bristol, Bristol, England. Feb 2016.

My former PhD student Kathryn Feller presented AFOSR-supported research at the Light and Life Symposium held at Scripps Institution of Oceanography, La Jolla, CA in May 2016.

b. Consultative and advisory functions to other laboratories and agencies, especially Air Force and other DoD laboratories.

We continually worked closely with Justin Marshall, University of Queensland, Australia, who is supported for joint projects by the AFOSR international office, Tokyo. We continue a number of collaborative projects on the biology and neurophysiology of linear and circular polarization. Justin and I jointly coauthored a book and numerous publications. Justin and his group also coordinated with us for field work at the Lizard Island Research Station in 2013, 2014, 2015, and 2016.

We continually worked closely with Nick Roberts, Bristol University, on modeling of polarization and other photonic structures in mantis shrimps. Nick's group published a number of papers on which I was a coauthor. Nick and several of his students joined us in the field in 2013, 2014, and 2015, and Nick visited my laboratory on several occasions and I visited his in 2016.

We also have worked intensively with Victor Gruev and his student Sam Powell at Washington University, Saint Louis, MO on polarization imaging and display systems, as detailed earlier. His team published a paper on which we were coauthors that was awarded the IEEE Donald G. Fink Award for 2016, and we have published other papers jointly. Viktor and/or Sam joined our team in the field in 2013, 2014, 2015, and 2016.

We continue to work closely with Roy L. Caldwell, University of California Berkeley, sharing experimental animals. Dr. Caldwell assisted us with critical field work in 2013, 2014, and 2015. Roy has been a coauthor on many of our important papers on polarization vision and polarization signaling in mantis shrimps.

We continued to join forces with Roger Hanlon, Marine Biological Laboratory, Woods Hole, Massachusetts, to complete our work on polarization sensing and reflections in cephalopod mollusks (squid, cuttlefish). This work was part of the PhD thesis of Alexandra Nahm.

We worked with Nate Morehouse, University of Pittsburgh on optical filters in the eyes of jumping spiders. The first publication from this work appeared in 2015, but additional projects are in progress.

We continue to stay in contact with my former postdoc Megan Porter, and she has continued to collaborate with us on several projects involving molecular genetics of polarized-light receptors.

We work with Sönke Johnsen on the physics and biology of polarization sensors, visual systems, and reflectors in a variety of animals. Sönke has been instrumental in helping with the work on the ecology and function of polarization vision.

c. Transitions.

None as of yet, other than our ongoing formal collaboration with the AFOSR-supported engineer, Viktor Gruev (nanotechnology and fabrication) and his student Sam Powell.

New Discoveries, Inventions, or Patent Disclosures

None, other than those already mentioned and described in detail above.

Honors/Awards

Elected Fellow of the International Society for Neuroethology (July 2014).
Visual Ecology awarded the 2015 PROSE award for Best Textbook in Biological and Life Sciences
Co-nominated for 2016 IEEE Donald G Fink Award (awarded in February 2016).

Figure 1A. Scan angles and rotation angles in *Neogonodactylus oerstedii* viewing polarized light fields. H, horizontally polarized fields; V, vertically polarized fields; R, right eye; L, left eye. All plots are as seen from a front view of the animal. Each black dot indicates data from one scanning movement. The top row shows scan angles; the bottom row shows rotation angles. The lines in each panel show either the primary scan direction or the axis of the rotation angle taken directly from the statistical analyses. The inset shows a right eye, seen from the front, to indicate the definition of scan angle and rotation angle. (From Durham et al., in review).

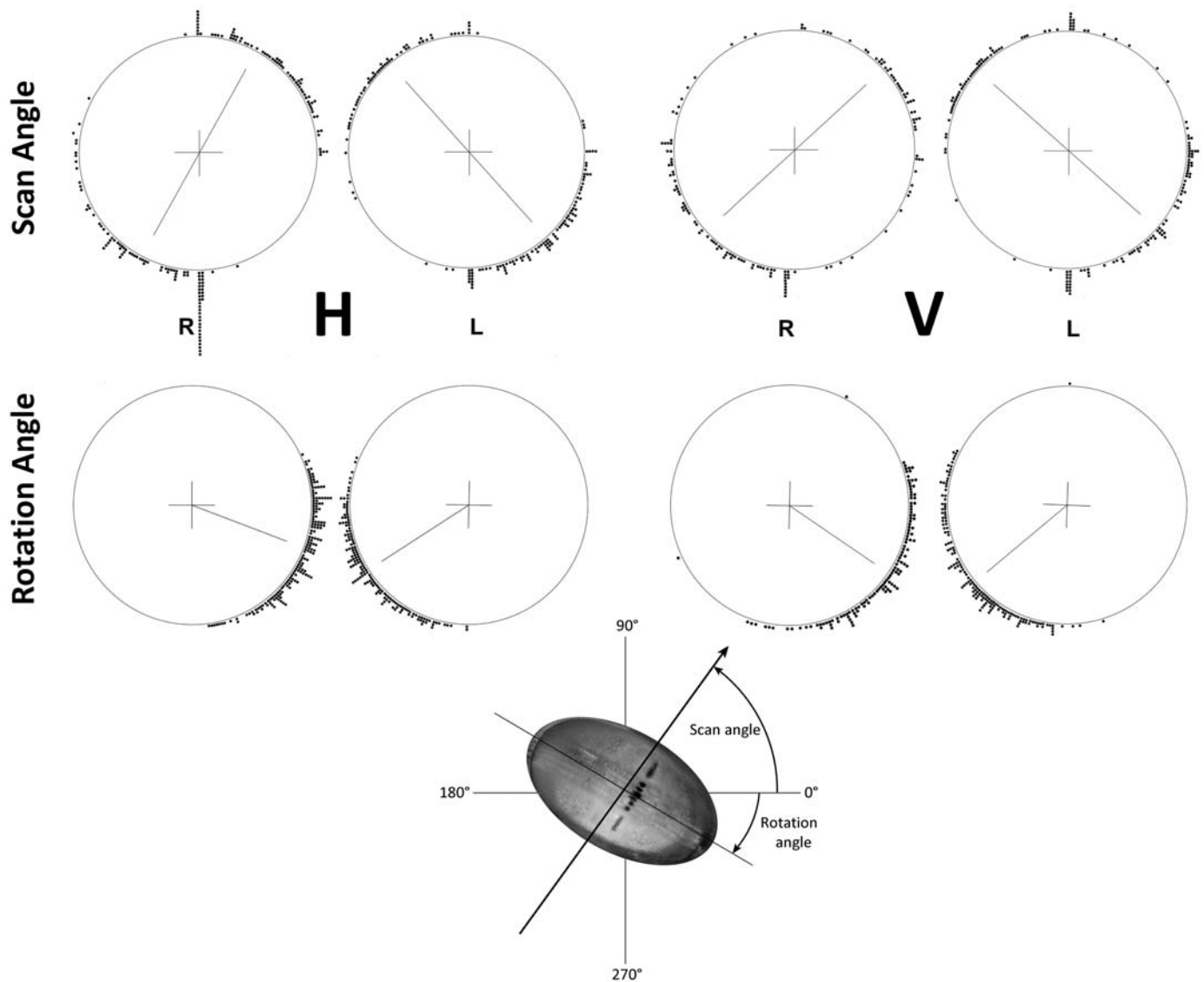


Figure 1B. Microvillar orientations in polarization-sensitive photoreceptor cells of *N. oerstedii* relative to a viewed polarized field. H, horizontally polarized field; V, vertically polarized field; C, depolarized field. All views are of the right eye from the front of the animal (see the diagram for keys to microvillar directions). Thin black lines, horizontal and vertical axes. Thick black line with arrowheads, angle of polarization. Gray line with thin arrowheads (SA), scan angle direction. Blue line (RA), average of start and finish rotation angle (from the horizontal, averaged in the same way as scan angles). The eye rotation angle was used to estimate the microvillar (mv) orientations in reticular cells (R) of the midband rows 5 and 6 and the hemispheres, as follows. Blue: ventral hemisphere (VH) R1,4,5mv. Green: VH R2,3,6,7mv. Purple, row 6 R1,4,5 mv, Row 5 R2,3,6,7 mv, and dorsal hemisphere (DH) R1,4,5 mv. Red, Row 6 R2,3,6,7 mv, Row 5 R1,4,5 mv, and DH R2,3,6,7 mv. The colored diagram shows typical magnified cross sections of rhabdoms and reticular cells in the eye as would be seen in life. The colored arrows indicate microvillar orientations in the correspondingly colored reticular cells. Note that reticular cell #1 is larger than cells R2 to R7. (From Durham et al., in review).

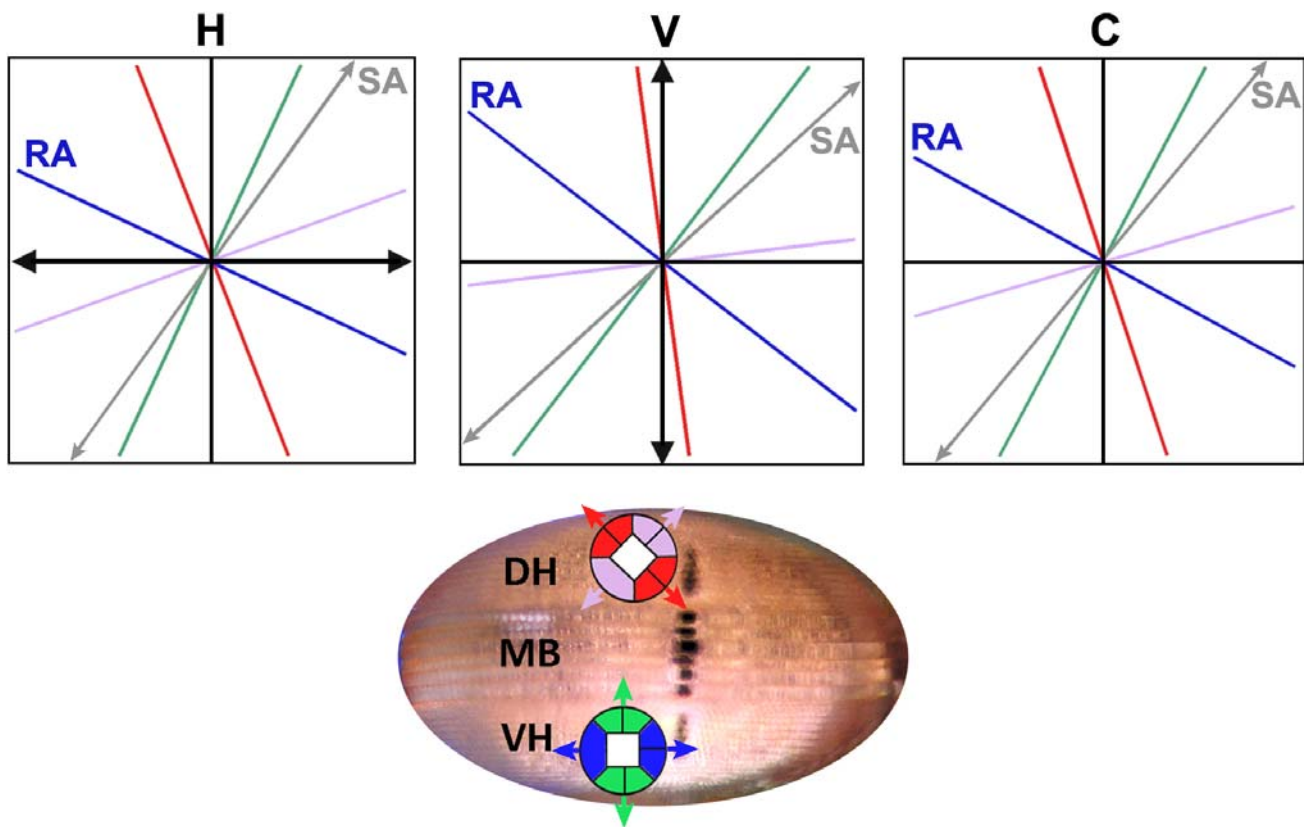


Figure 2A. Polarization scattering in water for use in underwater navigation. This figure defines the events that occur. A light ray penetrates the water surface (the blue grid) and is refracted and partially linearly polarized, with a vertical e -vector axis. If it is scattered by a particle, the scattered ray is polarized perpendicular to the plane containing the refracted axis and the scattering axis. The distribution of polarizations of along the various scattering axes allows us to compute the precise azimuth and altitude of the unrefracted image of the sun, and from this and a precise knowledge of time, the latitude and longitude of the observer can be determined.

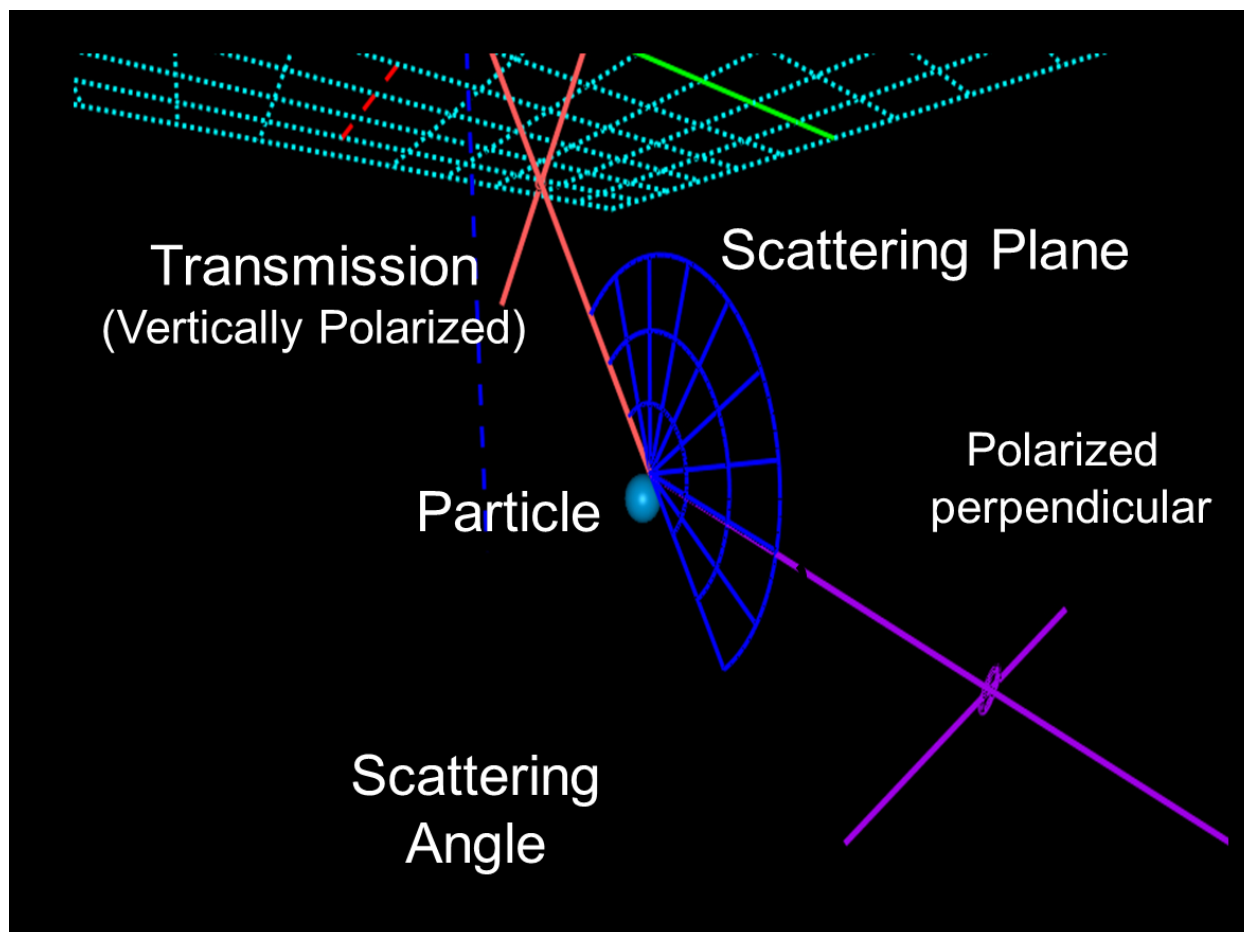


Figure 2B. Current levels of navigational errors obtained at various solar elevations and depths. Each panel shows the error in either elevation (top), azimuth (middle), or overall position (bottom) for various solar elevations and depths of measurement. Note that the system is fairly insensitive to both elevation and depth, and thus broadly useful throughout the day. Such a system could be extremely valuable to marine animals and to humans who wish to navigate accurately while not penetrating the water's surface. Grucev's team continues to improve the overall accuracy of their system.

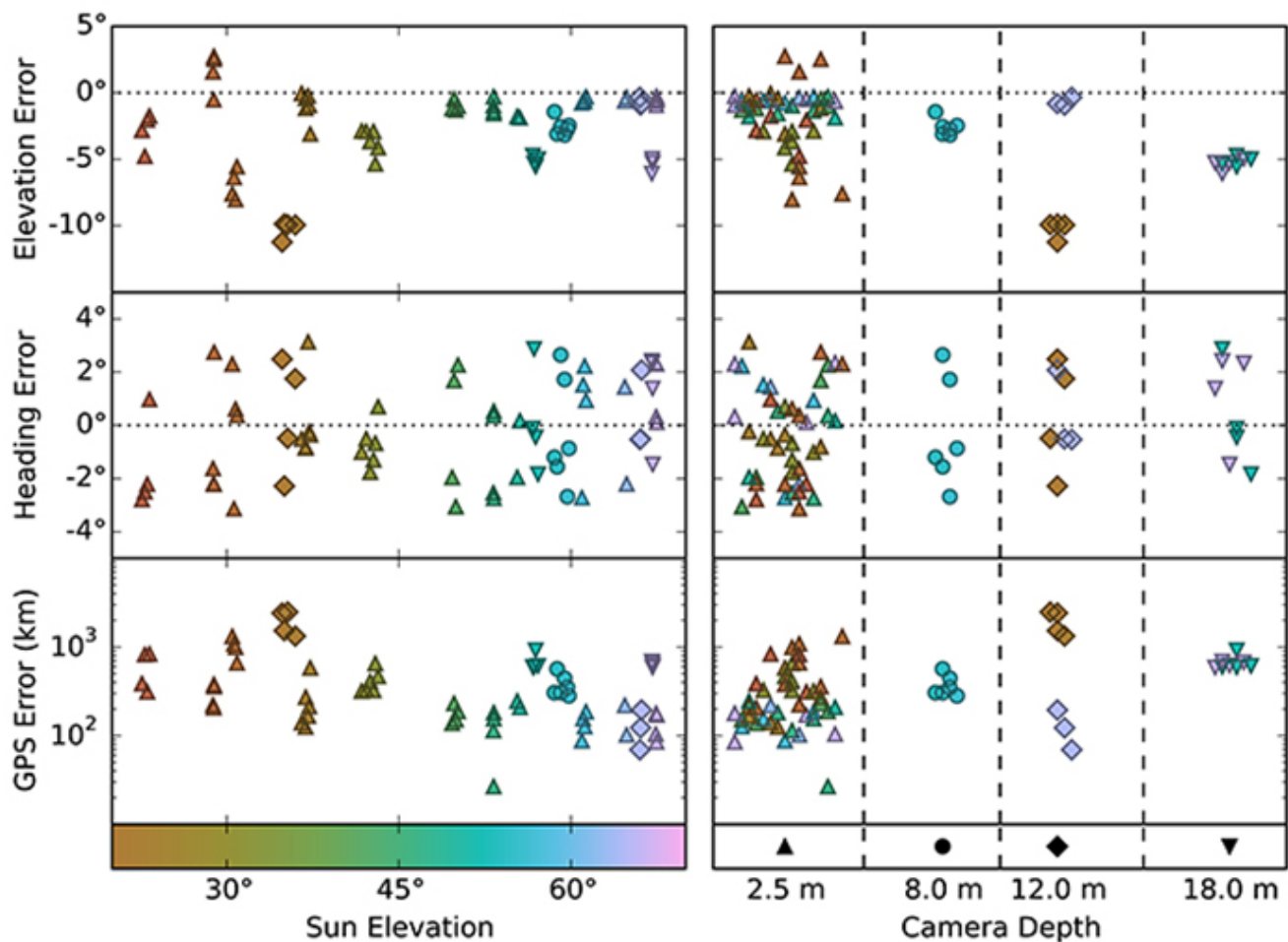


Figure 2C. Representative errors of underwater GPS geolocation using polarization in three locations: Hawaii, the Baltic Sea, and the Great Barrier Reef, Australia. The red dots show the spread of computed locations, with the green dot showing the actual location. The ellipses encircle the distributions of errors. These results are obtained with relatively primitive levels of analysis, which are being improved with better imaging and better error correction approaches.

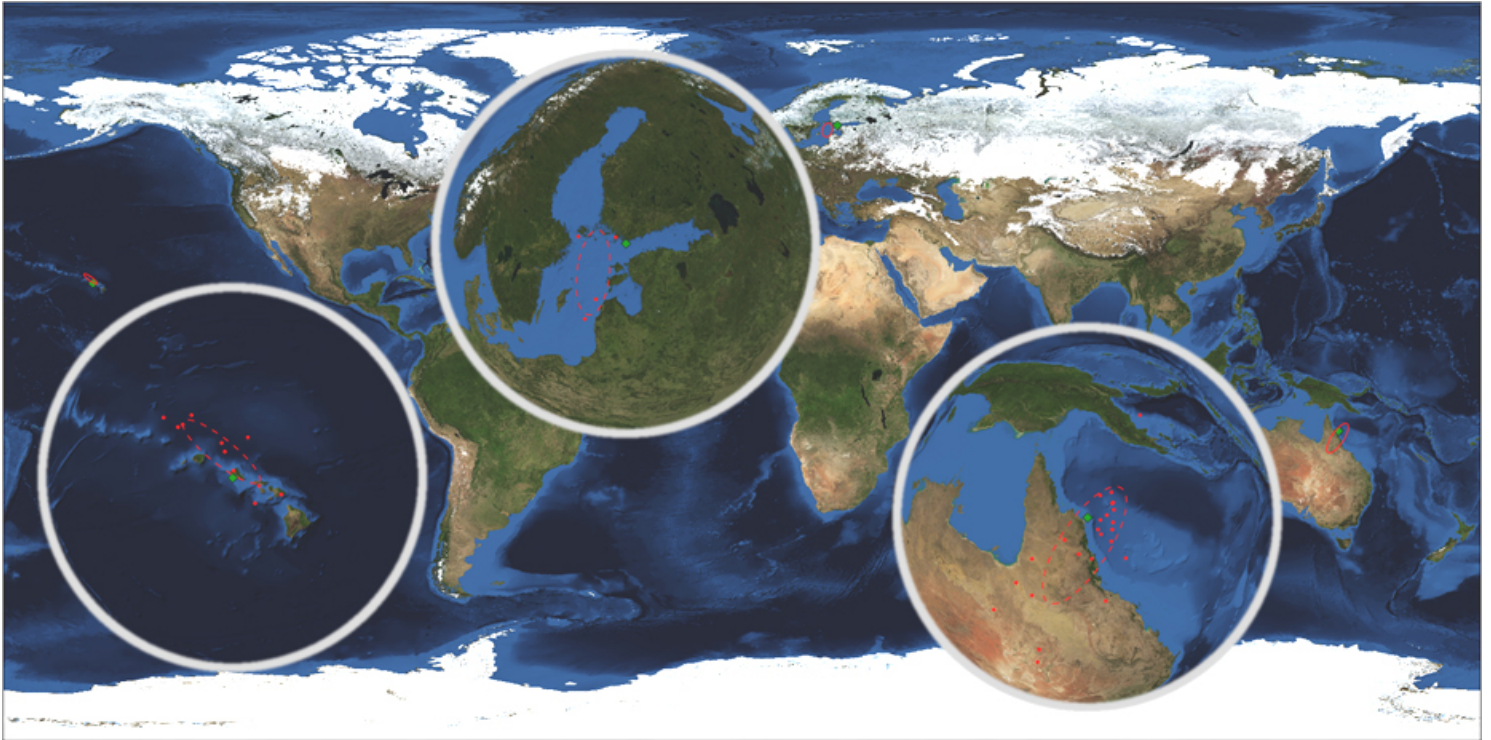
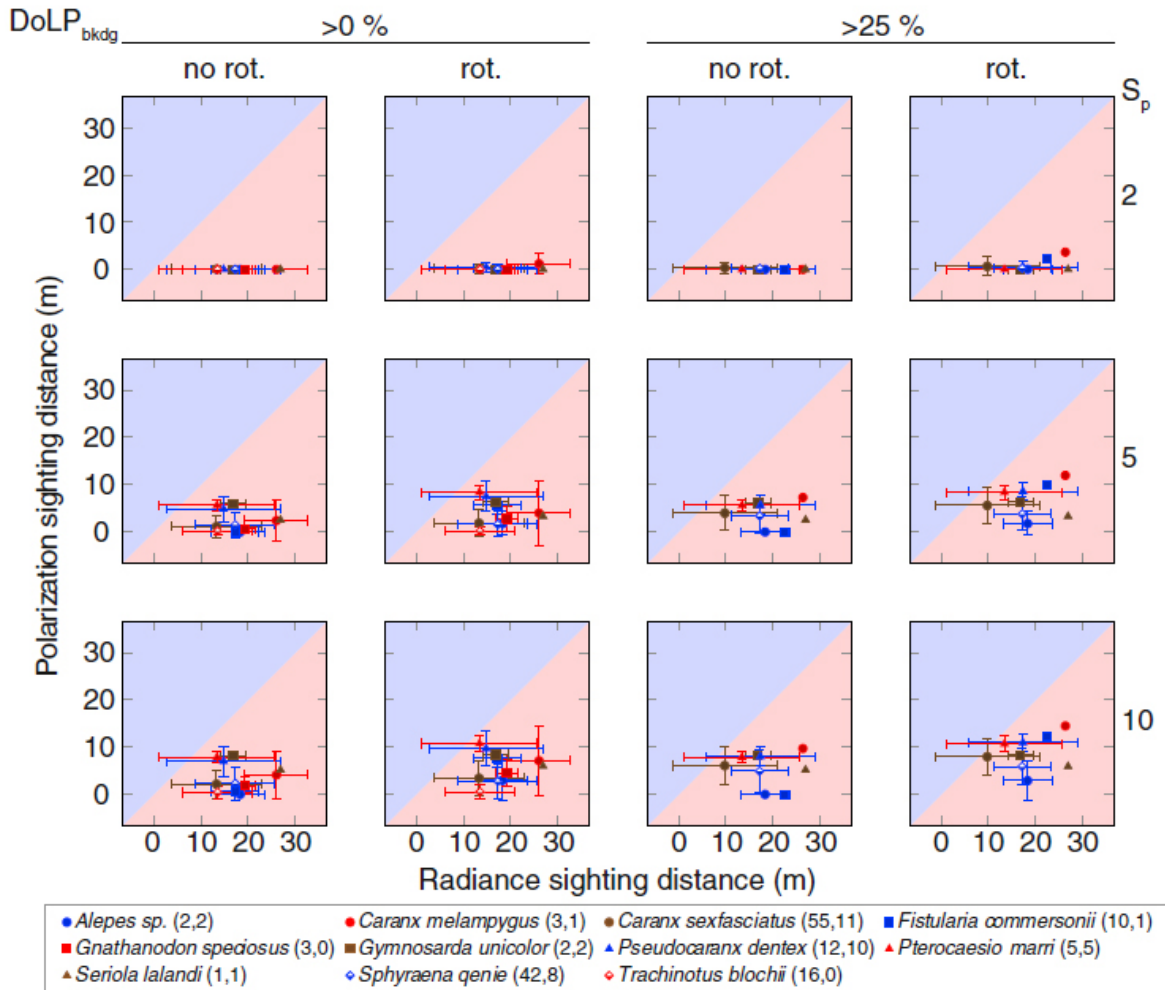


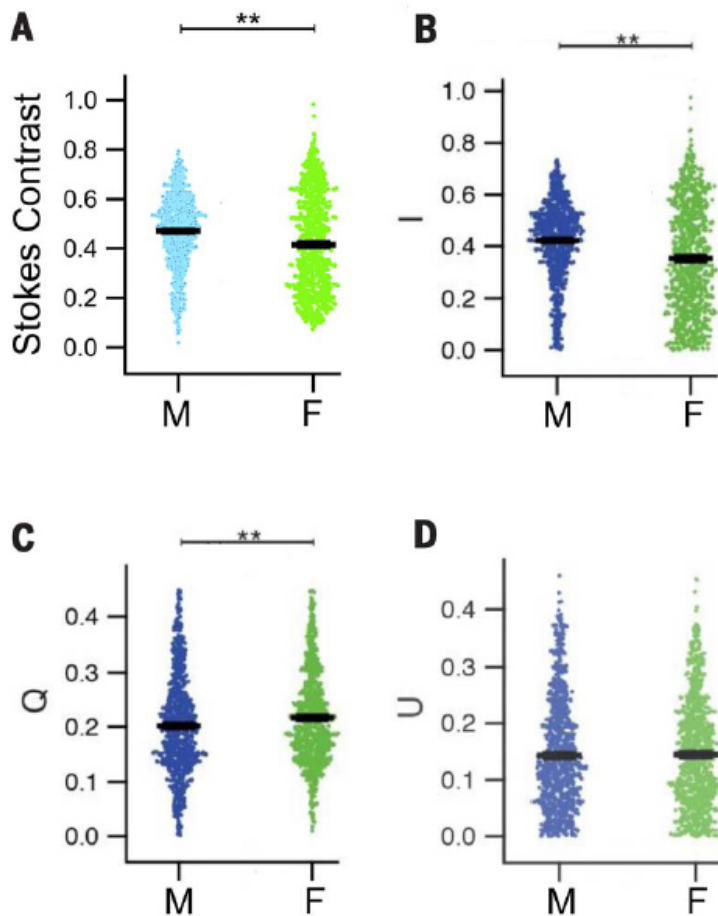
Figure 3A. Polarization and radiance sighting distances for viewing silvery fish (from Johnsen et al., 2016). See the caption below the figure for full explanation.



Polarization versus radiance sighting distances estimated from the radiance and polarization information captured by the polarization camera.

In columns 1 and 2, all images were included. In columns 3 and 4, only those images for which the background polarization (DoLP_{bkgd}) was greater than 25% were included. Within each pair of columns, two cases were considered: 1) the viewer's head was oriented such that the polarization photoreceptors are oriented horizontally and vertically ('no rot.'). 2) the viewer tilted its head (over a range of -45° to $+45^\circ$) such that the polarization sighting distance was maximal for each image ('rot.'). The polarization sensitivity of the microvilli S_p varies by row from 2 to 5 to 10. The two numbers following each species name in the legend are the total N and the N for which the background polarization was greater than 25% respectively. The error bars indicate standard deviation. Each graph is divided into two regions. In the pink region (which contains nearly all the data), the radiance sighting distance is greater than the polarization sighting distance. In the blue region, the opposite is true.

Figure 3B. Figure showing errors in a paper published in Science (2015) by Brady et al. That paper claims to show that polarization reflections reduce visibility of silvery fish. We show that their original data actually support the opposite conclusion (see caption for full explanation; from Cronin et al., 2016).



A compilation of figures adapted from Brady et al.

We do not include the diffuse mirror results for clarity. **(A)** Figure 2A from (1), which shows that the Stokes contrast W_s is less for the bigeye scad (F) than for the mirror (M). **(B)** Figure S4A from (1), which shows that the intensity contrast of the bigeye scad is also less than that of the mirror. **(C and D)** Figures S5A and S6A, which show that contrasts based on Q and U , the actual polarization parameters, are greater for the bigeye scad than for the mirror (7% and 2% greater based on tables S4 and S5). Together, (B) to (D) suggest that the pattern shown in figure 2A of Brady et al. is driven by intensity contrast rather than polarization contrast. $**P < 0.01$, based on the statistics used in (1).

Figure 4. Journal covers, 2014-2016, resulting from AFOSR-supported work.

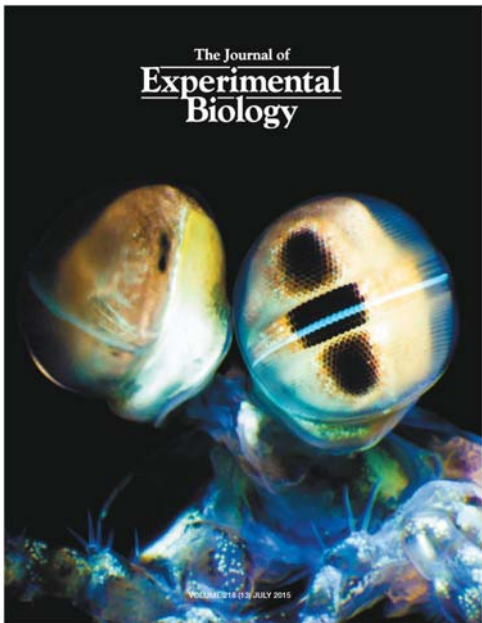
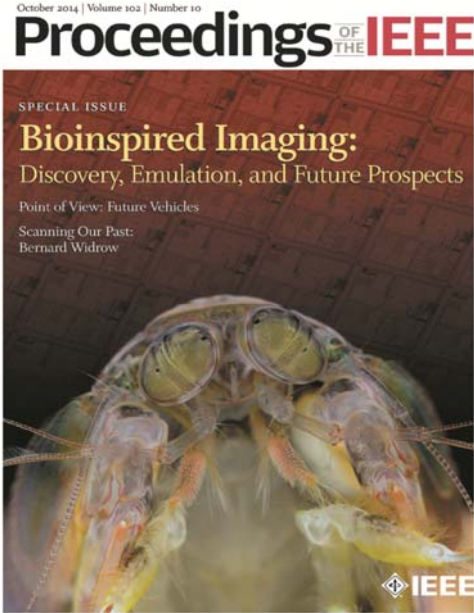
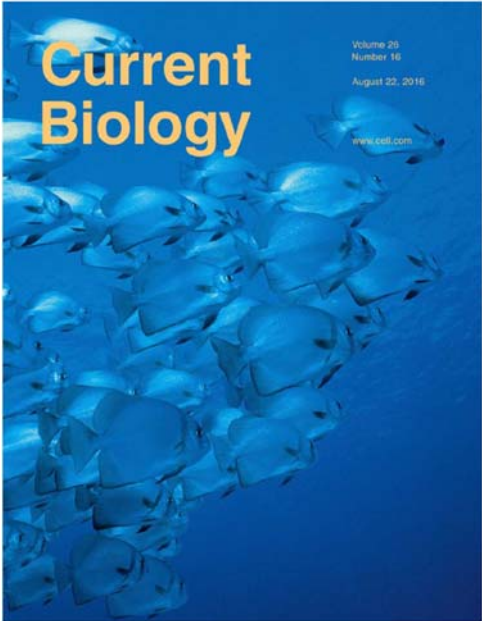
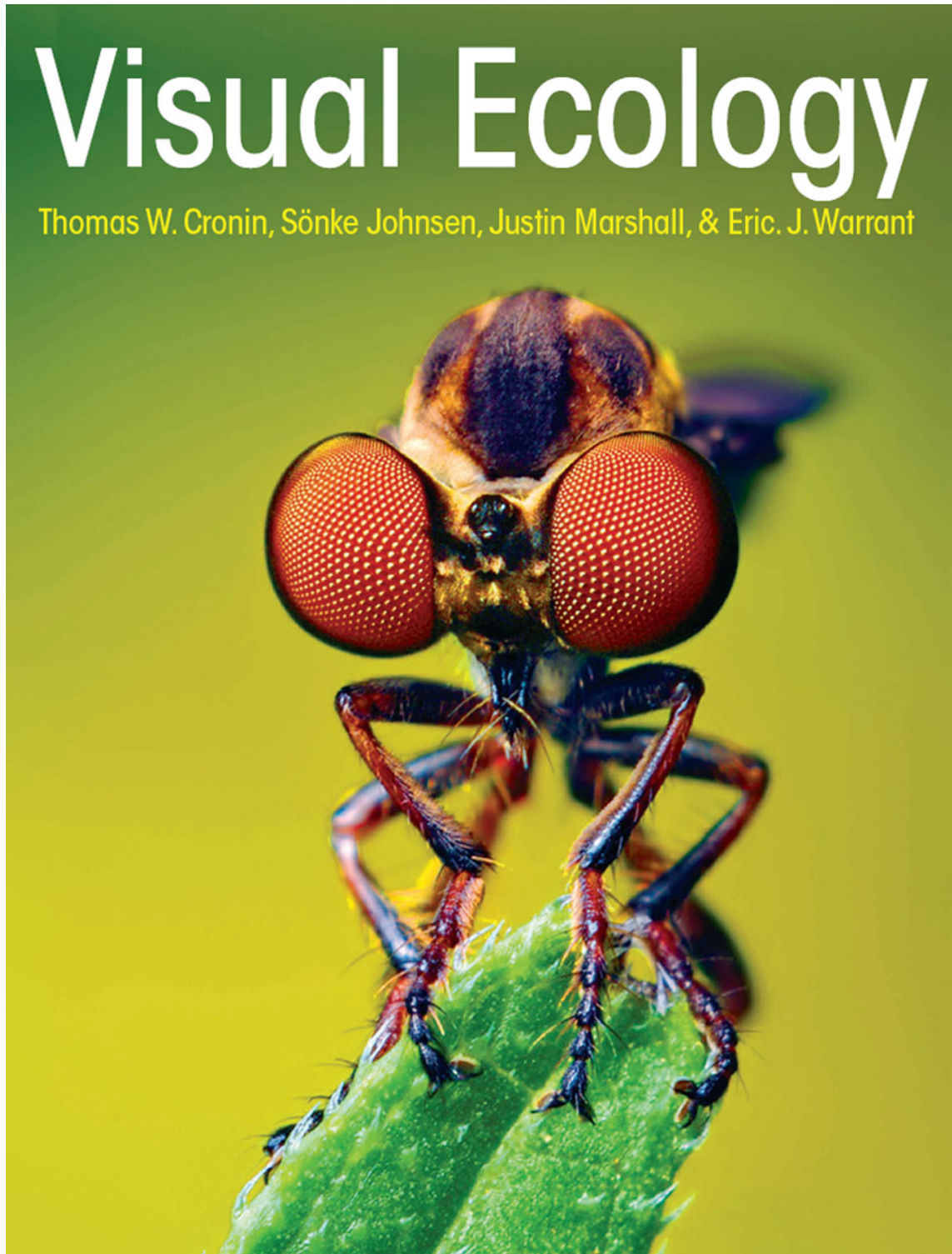


Figure 5. Book cover from *Visual Ecology*. Published by Princeton University Press in 2014, this book was a short-listed finalist for “Best Book in Biological and Life Sciences, 2015” and was awarded the 2015 PROSE award for “Best Textbook in Biological and Life Sciences”. Much of the information in this book was discovered through work from AFOSR-sponsored research.



Appendix: Work by Chan Lin, PhD

Dr. Lin has been investigating the neural organization beneath the compound eyes of the stomatopod crustacean *Squilla empusa* using a combination of neuroanatomical methods. These include osmium ethyl-gallate staining, reduced silver staining and Golgi impregnation that enable visualization of brain architecture at various levels of details, and fluorescent tracer injection, immunolabeling, and 3D reconstruction that allow functional interpretation of distinct brain regions. The major finding of his first year's work is that the overall neural organization of the stomatopod brain follows the malacostracan crustacean ground pattern, but with special modifications at various brain centers. As shown in the figures below, the stomatopod optic neuropils are characterized by distinct midband pathways (**Figure 2**), the hemiellipsoid body is elaborate (**Figure 3**), and the central complex is featured by a pair of noduli that have thus far only be found in pterygote (winged) insects (**Figure 4**). These findings suggest that stomatopods have evolved a more complex brain to better suit its needs in processing visual and other multimodal sensory information and commanding sophisticated behavior.

Figure 1. The brain of the stomatopod *Squilla empusa*. Selected brain areas of interest are illustrated on the right. These include optic neuropils (cyan), hemiellipsoid body (green), and central complex (orange). The two midband photoreceptor rows in the retina and their distinct axon projections in the successive optic neuropils are highlighted (yellow).

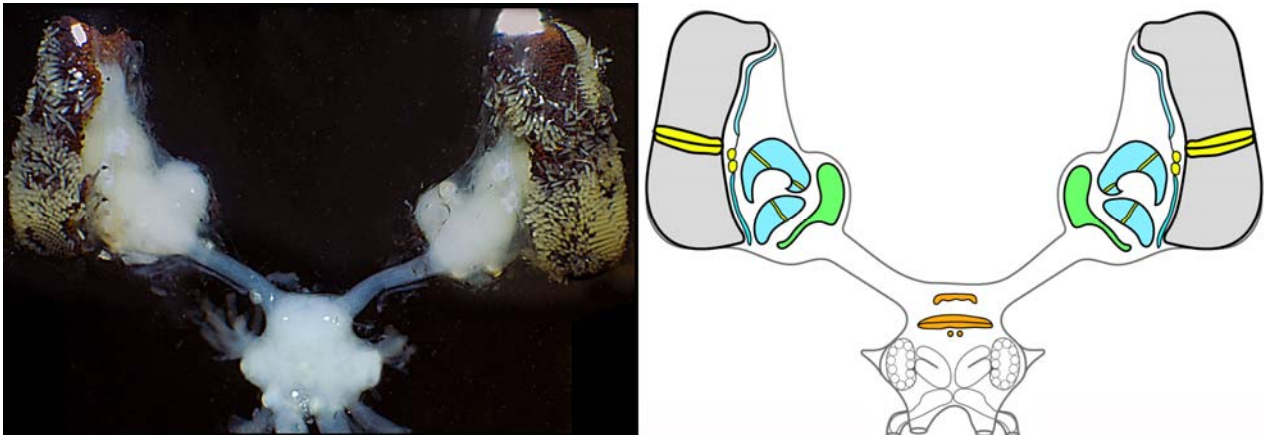


Figure 2. The *S. empusa* optic neuropils with midband specialization. Like other malacostracan crustacean and insect optic lobe organization, stomatopod optic lobes consist of three successive visual processing neuropils (lamina, medulla and lobula complex) that are linked by two axonal chiasmata. But stomatopod optic lobes have unique midband specializations. In *S. empusa*, photoreceptor projections from the two midband rows supply two sets of enlarged lamina cartridges (arrows in **A**, **B**) lying adjacent to the ventral hemispheric lamina (V-La). A gap in the lamina exists at the location of the missing lamina cartridges of the four rows of color-processing channels (arrowhead in **A**). This gap can be traced into the medulla with immunolabeling against synapsin (magenta) and α -tubulin (cyan; arrowheads in **E-G**). Columnar projections from the two midband rows can also be traced through the entire optic lobe with reduced silver staining (black arrowheads in **C**, **D**). D-La, dorsal hemispheric lamina; HB, hemiellipsoid body; Lo, lobula; LoP, lobula plate; Me, medulla.

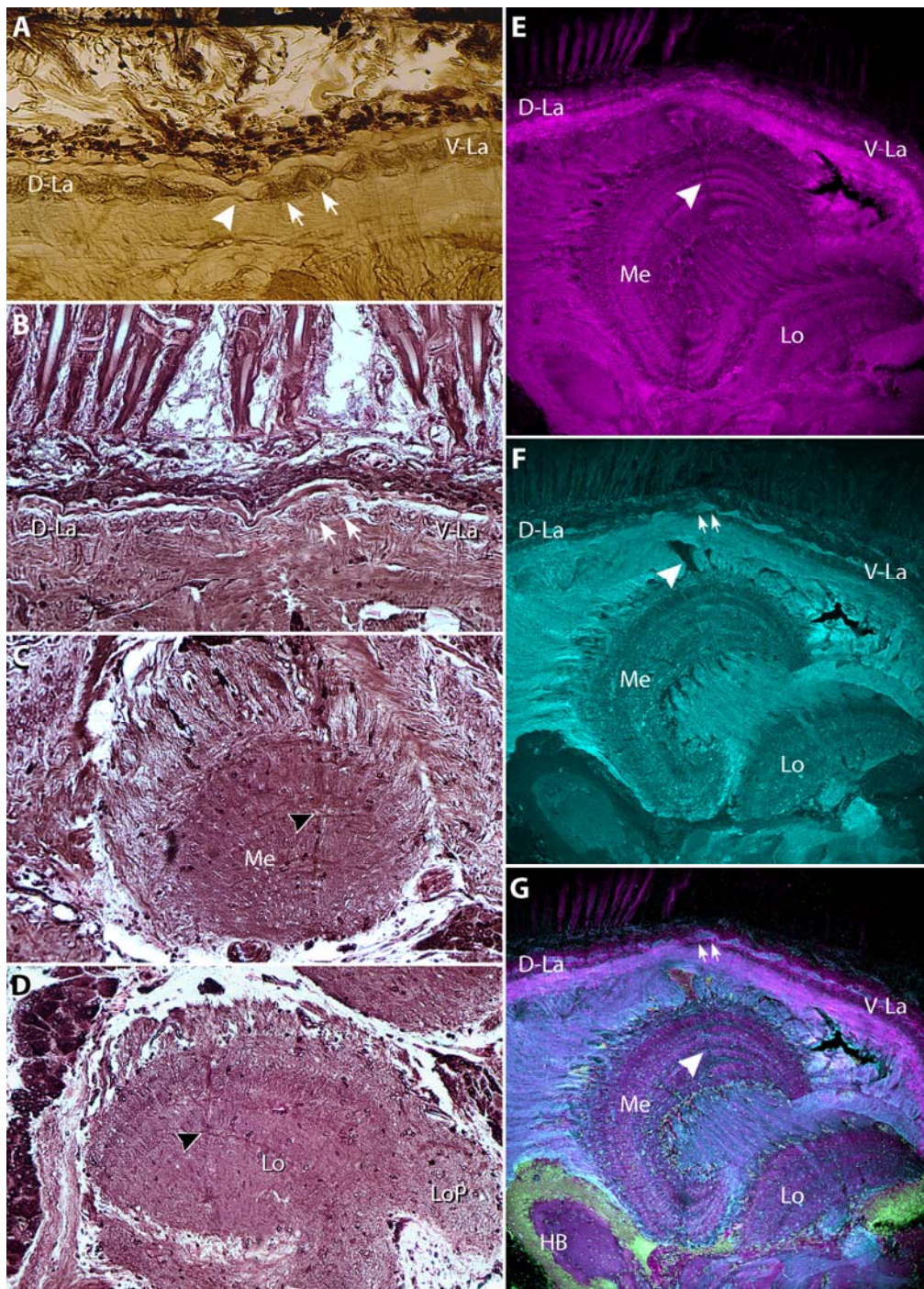


Figure 3. The elaborate *S. empusa* hemiellipsoid body. The crustacean hemiellipsoid body is evolutionarily homologous with the mushroom body of insects, which has been shown to be essential for olfactory learning and memory and spatial navigation. Unlike other crustaceans that have a hemiellipsoid body consisting of merely 2 subunits, the stomatopod hemiellipsoid body is greatly enlarged in size and further divided into at least 5 distinct layers (arrowheads in **B**, **C**). This organization is much similar to the mushroom body of honey bees, of which is also enlarged and divided into distinct regions that receive segregated neural inputs from visual, olfactory, and mechanosensory centers. Distinct output fibers originating from the stomatopod hemiellipsoid body can be seen (arrows in **A**, **C**). This is unique among all crustacean hemiellipsoid bodies. **A** and **B**, immunoreactivity against α -tubulin (cyan) and synapsin (pink), and nuclear stain showing the cell bodies (green). **C**, nuclear stain showing the cell bodies (green).

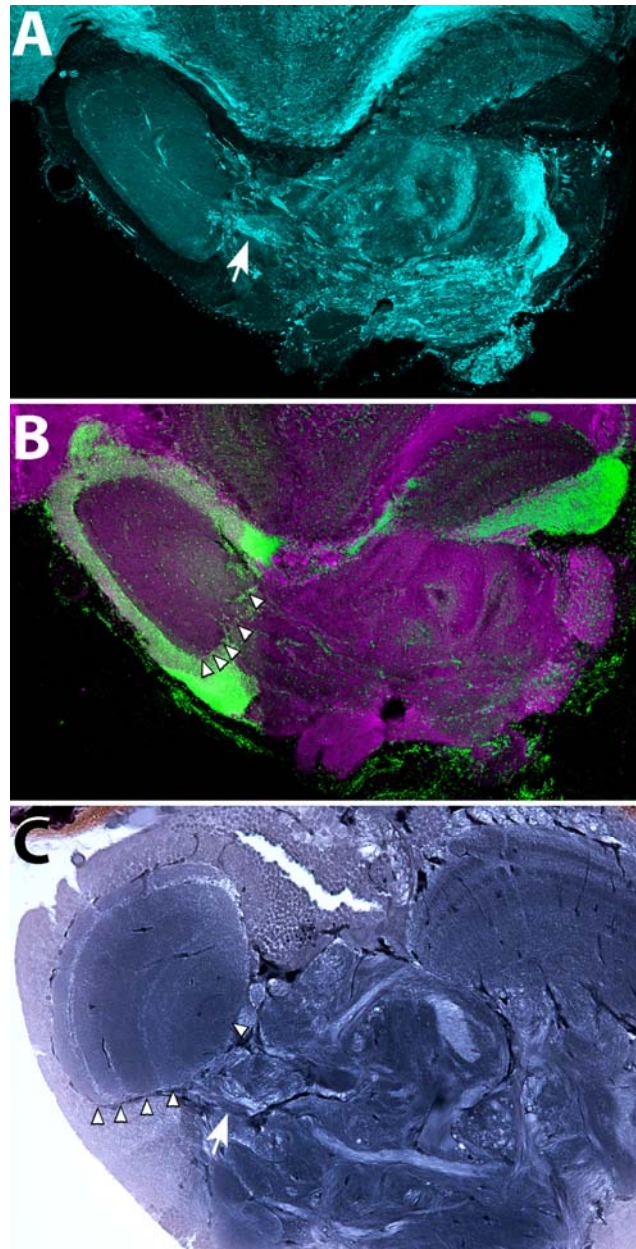
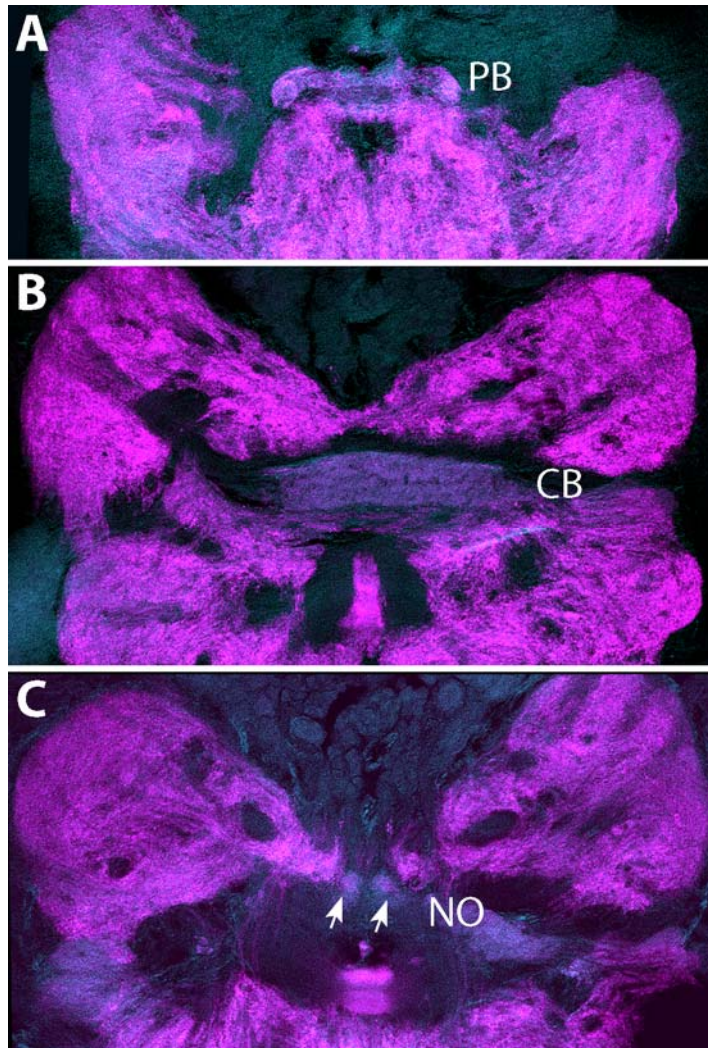


Figure 4. Neural organization of the *S. empusa* central complex. The central complex is a collection of arthropod brain midline neuropils implicated in sensory integration and pre-motor control. In the desert locusts *Schistocerca gregaria*, the entire range of polarized light e-vectors from 0–180 degrees is represented in the 16 vertical subunits of its protocerebral bridge of the central complex. While the central complex of insects and crustaceans share common developmental origins, the crustacean central complex found previously is more structurally simple, including merely a small v-shaped protocerebral bridge sits above a thin unstratified central body. Here we show that in *S. empusa*, the central complex is quite elaborate, including a widely spanned protocerebral bridge (PB in **A**), a large central body (CB in **B**) clearly divided into an upper and lower divisions similar to those of insects, and a pair of noduli (NO, arrows in **C**) that have thus far only been observed in pterygote (winged) insects presumably implicated in flight control. Pink, immunoreactivity against synapsin; cyan, fluorescent-labeled phalloidin.



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The full name of the principal investigator on the grant or contract.

Thomas W Cronin

Program Officer

The AFOSR Program Officer currently assigned to the award

Patrick Bradshaw

Reporting Period Start Date

06/15/2012

Reporting Period End Date

06/14/2016

Abstract

This final report (2013-2016) is a comprehensive summary of our efforts over the course of this grant. It focuses on the Cronin laboratory but includes work for the comprehensive four-team effort (also including Marshall's team in Australia, Roberts's team in England, and Gruev's team - subcontracted to Cronin - in St Louis, Missouri). Altogether the Cronin laboratory published some 36 papers, book chapters, or books from the middle of 2013 to the end of 2016 (the team as a whole has a total of some ~80-90 unique publications in this time). We have been completing our work on the opsin diversity in mantis shrimp eyes, with a strong focus on the opsins devoted to polarized-light vision, including our finding that polarized-light receptors contain an unusually large number of co-expressed opsin genes (this work has been ongoing since ~2007 or so). We have also greatly expanded our understanding of ultraviolet vision in stomatopods, including UV vision devoted to polarized-light analysis. The work has led to the discovery of a new class of filters used in animal eyes to control the detection of multiple bands of ultraviolet light, including polarized ultraviolet, published in 2014 and 2015. We have continued to develop field-capable, user-friendly, real-time polarization cameras in collaboration with our subcontractor Viktor Gruev and his students, used for visualizing environments, terrain, and animals in natural settings, and also extending this work to

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preliminary studies of polarization patterns in stomatopods and cephalopods. We collected hours of polarization video in marine and terrestrial environments and have just published a paper on the polarization properties of fishes in clear marine waters in the prestigious journal *Current Biology*. From this work, we have finally begun to work out the utility and the limits of polarization imaging and polarization camouflage in marine animals, which led to a major critique published this year in *Science* (and to a future review in the *Journal of Experimental Biology*). The imaging work was awarded IEEE's 2016 IEEE Donald G. Fink Award. The Gruev team is also exploring the possibility of using polarization imaging as a tool for underwater navigation. The team as a whole has met repeatedly to conduct research every year and to plan ahead, including a meeting with the AFOSR program fundees at Eglin AFB in October 2013 and 2014 and in Arlington in 2015. We conducted joint field trips to the Great Barrier Reef in 2013, 2014, and 2015. In addition to this, Cronin and his students and postdoc attended numerous meetings nationally and internationally in 2013-2016.

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No

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Do you plan to pursue a claim for personal or organizational intellectual property?

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None

Change in AFOSR Program Officer, if any:

None

Extensions granted or milestones slipped, if any:

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Research Objectives

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